

Response to Comment on "Why Are There So Many Species of Herbivorous Insects in Tropical Rainforests?"

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Norton and Didham suggest that differences in plant abundance between tropical and temperate forests may influence the host specificity of herbivores in these forests. We agree in principle but show that this is likely only for very rare plant species in tropical forests. Studies of herbivores hosted by rare plant species would help our understanding of tropical plant-insect interactions.

Norton and Didham (1) argue that differences in plant abundance between tropical and temperate forests may limit the general conclusion that herbivore diversity scales directly with host plant diversity. They point out that our study (2) did not include locally rare tree species. Our temperate/tropical comparison was standardized for sample size and plant phylogeny but not for plant abundance and, indeed, there are more rare tree species in

tropical forest, including forests we studied (Fig. 1A).

Extremely rare plant species are expected to host fewer specialists, and herbivore species overall, as they represent a rare and scattered resource difficult to use by herbivores. However, it is not known what resource abundance is limiting for herbivorous insects. Specialized herbivores may be few in communities colonizing rare plants with unpredictable distribution in space and time, such as annual herbaceous species limited to brief, early stages of ecological succession after unpredictable disturbance events (3). It is less clear what represents extreme rarity for herbivores from large perennial plants, such as trees. Our study suggests that there is no impact of plant abundance on the species richness or the host specificity of their leaf-chewing communities for plant abundance characterized by the basal area from 0.01 to 10 m²/ha (Fig. 1, B and C). This range included 117 out of the 151 plant species from 1 ha of the tropical forests (Fig. 1A). However, our study,

similar to virtually all others from tropical forests (4), did not include rare species of plants.

Apart from methodological difficulties of sampling rare plant species for herbivores, there are other complications in the study of the effect of plant rarity on herbivores. Most insect herbivores prefer young foliage (5, 6). The biomass of young leaves may be a better measure of resource abundance than the total plant biomass, which is mostly inedible to most of the herbivores. Low seasonality of leaf flush typical for many trees in tropical rain forests makes this resource available at lower densities for a longer time, compared with young leaves produced during a synchronized leaf flush in temperate forests. Young foliage in the nonseasonal tropics thus supports more herbivore generations, but possibly at lower population sizes, than similarly abundant but seasonal resources in the temperate forests.

The plant species with extremely high or low densities may also be unusual in other aspects of their ecology. For instance, monodominant forests offer an opportunity to study tropical herbivores feeding on exceptionally common tree species (7). However, these forests exist only in low-nutrient environments, such as sandy or swampy soils, which can also influence the quality of plant resources for herbivores. This is probably why the diversity of insect herbivores in these forests is low (8) and why they are not exceptionally host specific, contrary to expectations for an abundant resource (9).

The impact of plant abundance on herbivorous insects depends also on the colonization ability of the insects, which varies among species and clades. For instance, aphids are inefficient colonizers, which may explain their low diversity in tropical forests (10), whereas Lepidoptera typically disperse hundreds of meters to several kilometers in their lifetime,

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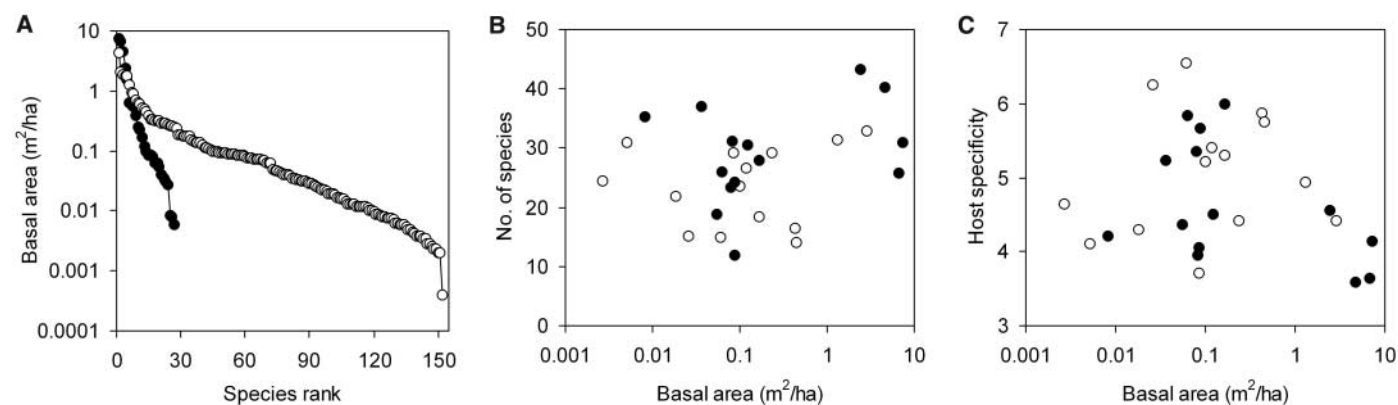


Fig. 1. The abundance of woody genera in temperate and tropical forests (A), and the relationship of plant abundance with species richness (B) and host specificity (C) of their folivorous herbivores. Plant abundance, expressed as basal area, that is, the combined area of the cross-section of all conspecific trees at 1.5 m above the ground, was estimated in 1-ha plots in the temperate (dots) and tropical (circles) forests at the study sites used by Novotny *et al.* (2, 14). The number of folivorous species per 100 m² of foliage

and the average number of host plant species of these herbivore species are shown for two sets of 14 tree species from respectively temperate and tropical forests (2). There is no correlation between the plant basal area and either of the herbivore variables in any of the two types of the forest (Pearson r , $P > 0.1$, both for the correlation using plant species as independent data points and for the independent contrasts analysis, taking into account statistical nonindependence of tree species due to their shared phylogeny).

although data from tropical forests are rare (11). Good dispersal ability of many tropical folivores is suggested also by their rapid colonization of pioneer trees recently established at disturbed sites (12) and of isolated plants in the forest (13).

Norton and Didham (1) point to an important, but for its technical difficulty so far neglected, problem—namely, the effect of plant rarity on the composition and ecology of herbivore communities in tropical forests. Finding what represents a rare species to a tropical insect

herbivore will be important and interesting, but not easy.

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23 January 2007; accepted 27 February 2007
10.1126/science.1139702